PROTO-FIDDLERS AND FIDDLERS : PATHWAYS TO WAVING IN INDIAN BRACHYURAN CRABS[1]

RUDOLF ALTEVOGT[2]

(*With four text-figures*)

The visual signalling gestures of the brachyuran crabs *Macrophthalmus tomentosus*, Souleyet (Grapsidae), *Dotilla blanfordi* and *D. myctiroides* (Ocypodidae, Scopimerinae) are described and analyzed by cinematography. In comparison with the waving of true fiddler crabs (genus *Uca*, Ocypodidae, Ocypodinae) one finds an ascending series of complexity in these communication signals so that the said crabs may serve as examples of evolutionary pathways to waving.

Almost a century ago, Alcock (1892, 1902) gave the first account on Indian fiddler crabs which he had observed in the field on the banks of the Godavari and Kistna rivers. Almost twentyfive years ago, I published "some studies on two species of Indian fiddler crabs, *Uca marionis nitidus* Dana and *U. annulipes* Latr." (1955) in the very Journal which we are celebrating by the present diamond jubilee volume. Since then quite a bulk of information has been obtained on the systematics, behavioural ecology and physiology of these most highly evolved brachyuran Crustaceans (for literature upto 1974 see the veritable "bible" on fiddler crabs by Crane, 1975). From the findings of a hoard of enthusiastic Uca-students and scholars quoted in the monumental volume by Crane and other sources listed below, it can safely be concluded that

1) the name giving visual gesture (fiddling, beckoning, waving the great claw by the males) serves semantic purposes informing the conspecific rival to keep away and the potential sex partner to feel appeased and willing to mate,

2) there is a graded series of complexity in the type of waving in the ninety-odd species of true fiddlers of the genus *Uca* reaching from a primitive up-and-down movement of the claw (as in *Uca batuenta* from South America, Altevogt and Altevogt, 1967a) to the extraordinary rotation waving (as in *Uca insignis* from the Eastern Pacific, Altevogt and Altevogt 1967b),

3) that corresponding homologous vibratory signals are produced by tapping claws or legs against the soil when underground in the crabs' burrows at night or under dense vegetation obstructing visual signalling.

While the intriguing wealth of various types and levels of waving in the true fiddlers has attracted numerous authors (including a good number of my students:
Von Hagen 1962; Gunther 1963; Nosler 1963; Korte 1966; Feest 1969; Jansen 1970; Heinrich 1971), the evolutionary prestages of true waving in the lower ranks of Crustacea have little been worked upon (though some hints to and considerations of this phenomenon can already be found in Altevogt, 1957a, b). Also Schone & Schone (1963) as well as Wright (1968) have

[1] On the 70th anniversary of Prof. Harald Stumpke, alias Gerolf Steiner in Mairuwilli, Black Forest.

[2] Department of Physiology and Ecology, Faculty of Biology, Munster University, Federal Republic of Germany.

dwelt on this subject. It is for this reason that in the following pages some Indian proto-fiddlers shall be treated and compared to some true fiddlers of India. The relevant data were recorded on several trips to crab habitats along the Indian coasts from north of Bombay down to Cape Comorin and up to Diamond Harbour/Calcutta during the years 1970-1976. Recording was done by cinematography (24-64 frames per second, Bolex H 16 reflex, 16 mm, Ektachrome), and still photography. Thanks are due to Professor Dr. H. O. von Hagen, Marburg, for determining the Macrophthalmus species, and to Miss M. Hans for frame-to-frame analysis and drawing.

From my selected list of proto- and true fiddlers, undoubtedly *Macrophthalmus tomentosus* (earlier known as Mareotis), Souleyet (Grapsidae), belongs to the most primitive fiddlers, followed in ascending order by the two *Dotilla*-species *D. blanfordi and D. myctiroides* (Ocypodidae, Scopimerinae) and the true fiddlers of the *Uca*-type of which *U. urvillei* will be dealt with here. The latter was chosen because its waving type and display are among the simplest and they have so far not been treated in detail (A rough sketch of waving in *Uca urvillei* from Inhaca Island, Mozambique, was given by Mcnae and Kalk, 1958, and Crane, 1975, reports observations from Tanzania and data taken from films on two individuals during August).

Waving in **Macrophthalmus tomentosus**

This is a rather slow affair compared to the real thing in a true fiddler of a somewhat high evolutionary level as, for instance, *Uca annulipes* (see Altevogt 1955, 1957a, and film 1957). From my movie scenes taken in February/March 1976 near Adyar/Madras we find that in *Macrophthalmus tomentosus* the average waving gesture lasts 2.4 seconds (n = 18). From the resting position of the two claws in front of the body and close to the ground, the signalling gesture starts by an asynchronous movement of one claw (see fig. 1, frame 12), thus giving way to an upward movement of the other one (frames 17 to 28). Meanwhile, also the other claw performs a lifting motion (frames 28 to 33). In reaching the apex, both claws catch up with each other so that in the highest position both claws are fully stretched out above the crab's body (frame 39). Lowering the raised claws to the ground and bringing them back to the resting position in front of the mouthparts complete the waving gesture (frames 44-54). It is, then, primarily a vertical wave.

We must note, however, that the temporal pattern of lifting and then lowering the chelae shows an important feature in the 3 to 5 jerks in the raising, while no such intermittent short stops are found in the downward movement. Hence, the conspicuous element in the whole gesture rests in the downward stroke (a finding similar to that in *Dotilla blanfordi*—see Altevogt, 1957b—and to *Dotilla myctiroides*, see below, and to that in many Uca signallings). While on the average the jerking upward movement lasts 2 seconds, the downward emphasis takes only a flash of 0.4 seconds. We have not seen much alteration of this temporal pattern even when a female or male conspecific was close by. This fact may also be taken as a criterion of primitivity, as in true fiddlers the rate and type of waving become more rapid and complex if a prospective sex partner approaches (see Von Hagen, 1962, 1968, and the films by Altevogt and Von Hagen, listed in the appendix). Moreover, in advanced stages of courtship (i.e., higher excitation levels) of most *Uca*-species, the ambulatories are lifted off the ground in a species-specific manner and take part in the

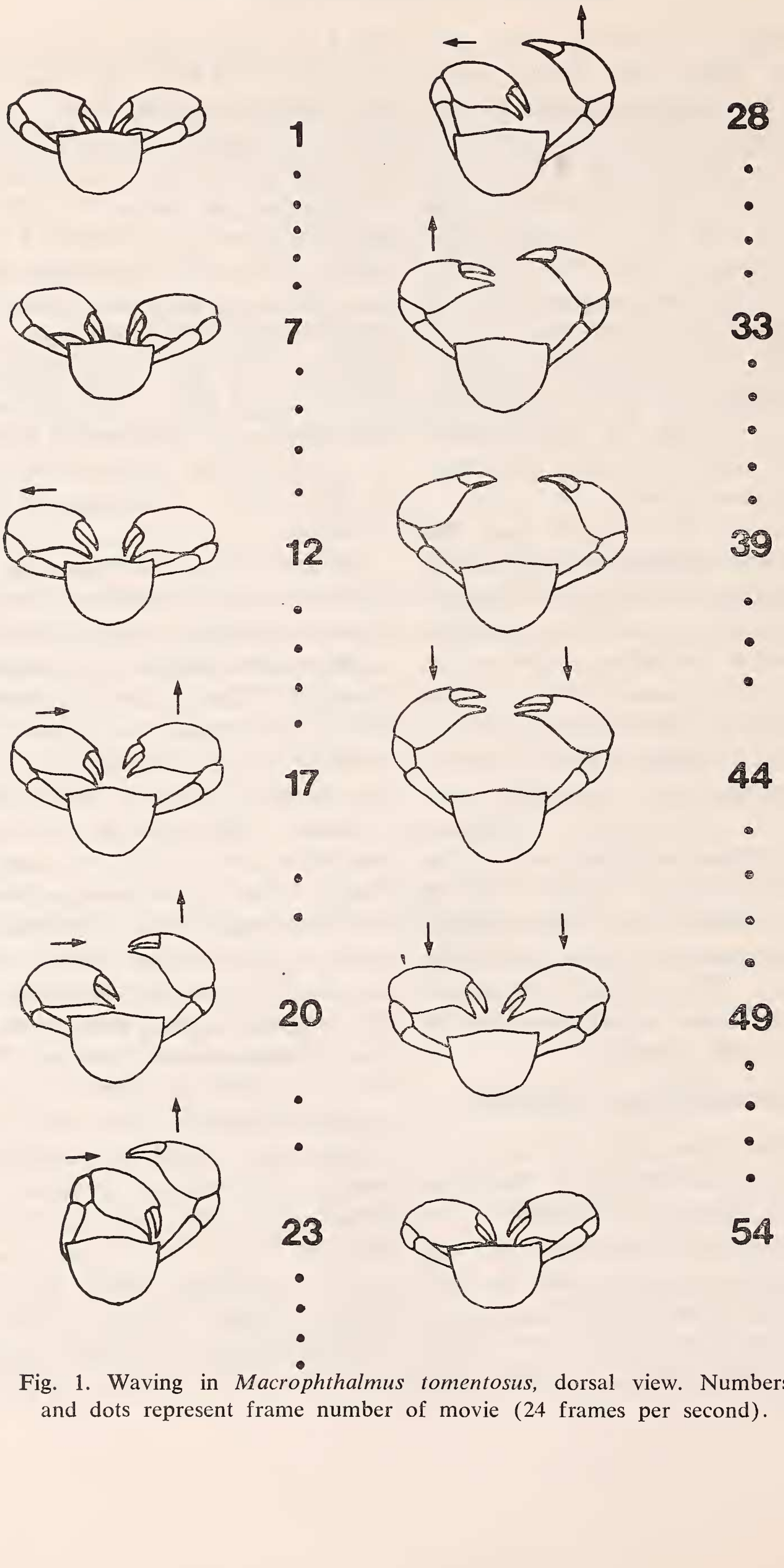

Fig. 1. Waving in *Macrophthalmus tomentosus,* dorsal view. Numbers and dots represent frame number of movie (24 frames per second).

signalling. No leg raising as in *Uca annulipes, insignis* and others was seen in about 50 individuals of *Macrophthalmus* observed in various stages of excitement. These findings suggest that waving is derived from a locomotory movement because in *Macrophthalmus,* where nature has presented us with a prefabricated slow motion example, the movements of the claws are not at all synchronous at the start, but follow the ancestral style of activating the ambulatories (and the chelipeds as derived walking legs, too) in a crosswise manner. Hence, the waving gesture starts with one claw (see also Altevogt 1972, p. 459 ff.). Incidentally, Crane hypothesized that the vertical wave (as in *Macrophthalmus*) originated from a feeding movement (as in a mud sifting *Uca*-species) while the horizontal wave of several *Uca*-forms would have derived from a threatening gesture in which the claw as a fighting weapon would be shown (1975, p. 523/524 and fig. 87). Earlier, Hediger (1933) had advanced similar ideas about the common root of threatening and waving. It should be noted here that in *Macrophthalmus* both claws are very much similar, if not equal in size.

While in a non-waving *Macrophthalmus* the claws are drab earthen-coloured they tend to become whitish in a signalling animal. This also would be more compatible with a sex-attractant function than with a threatening gesture. In a *Macrophthalmus*-species from Port Swettenham (Malaysia), probably *M. pacificus* Dana, Tweedie (1954) reported bright blue claws and has seen them performing waving movements with both chelae. We have not seen any copulations in *Macrophthalmus* so that the connection between waving and sexual success remains still to be shown (though it is strongly to be inferred from a bulk of findings in other Crustacea Brachyura).

Waving in **Dotilla myctiroides**

While the waving pattern of *Dotilla blanfordi* had been analyzed by frame-to-frame-studies in 1955 (Altevogt 1957b), the typical gesture of *D. myctiroides* had not been covered. The present data were recorded near Panjim (Goa) and Adyar/Madras from February to April 1976.

There are two types of claw movements in *Dotilla* which may easily be confounded by the inexperienced observer: a) the "dance of triumph" after a mock or real fight against an opponent (described in detail for *D. blanfordi* in Altevogt, 1957 a and b) the courtship wave which is, among others, recognizable by the conspicuously bleached chelae. While these are dull brownish-grey in the non-sexual animal they become bluish-white in the sexually aroused male (photograph in Altevogt, 1957b, p. 386). Only the latter type will be dealt with here.

Similarly to the waving in *Macrophthalmus* described above, in *Dotilla myctiroides* the downward component is the most emphasised element of the gesture lasting only 0.08 seconds, while the lifting movement takes 0.13 seconds (averaged from 22 waves in 20 specimens). As can be seen from figure 2 (lower graph), waving gestures follow one another at intervals of 0.17 seconds on the average with a shortest recorded interval of 0.13 seconds. This is slightly superior than the temporal pattern of the *D. blanfordi*-wave where the shortest interval is about the same, but lifting the claw lasts slightly longer ($>$ 0.17 sec), which also applies to the lowering it in the downbeat (about 0.1 seconds).

The spatial components of the *myctiroides*-wave resemble those of the *blanfordi*-gesture and may be seen in fig. 2, upper graph. It should be noted that in both species the claws'

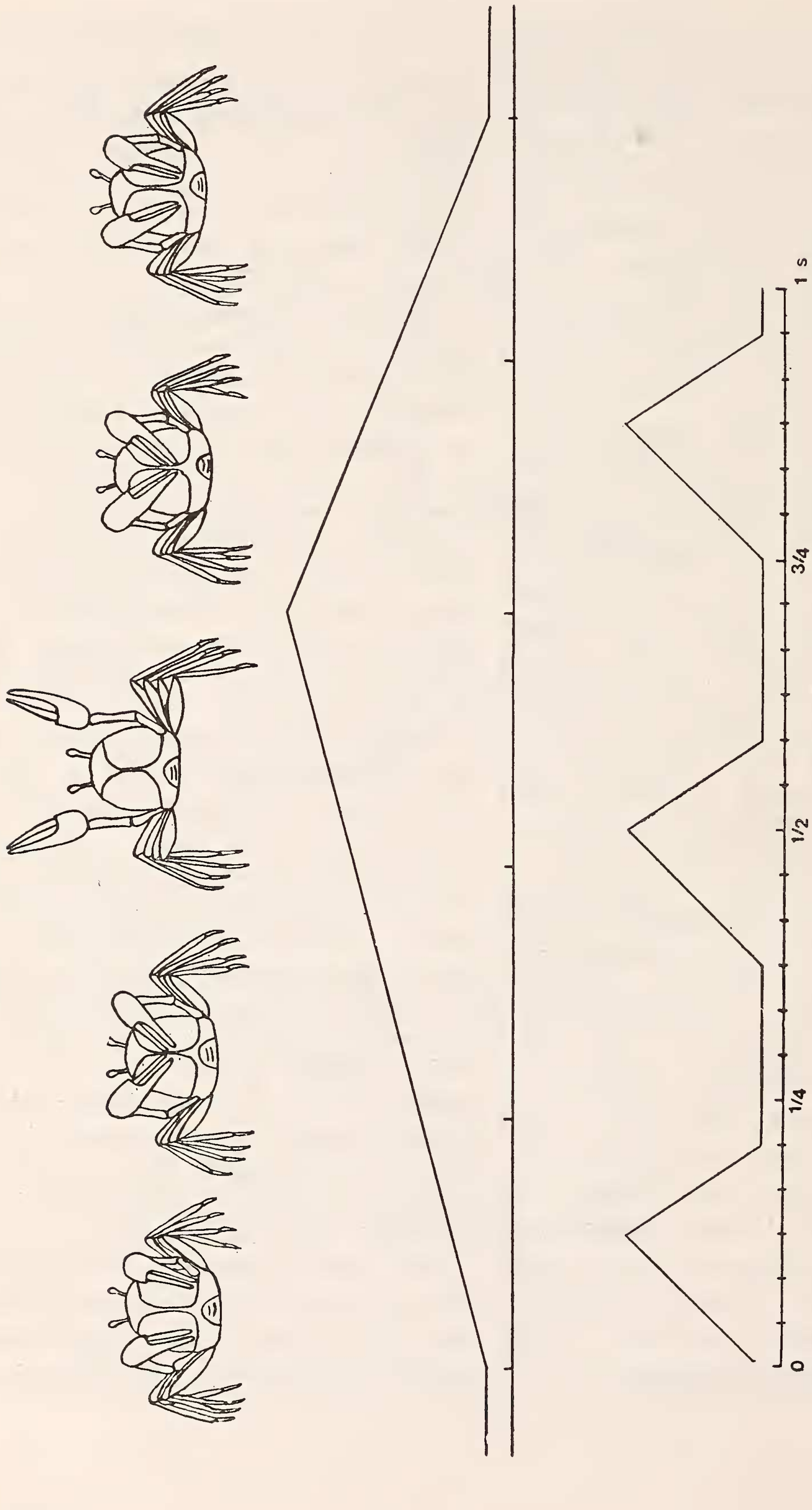

Fig. 2. Waving in *Dotilla myctiroides*, frontal view. Time Scale: 1/24 second.

upward movement is accompanied by a body raising on tip-toes on stretching legs, thus rendering the signalling even more conspicuous. Our recordings at 64 frames per second do not reveal any asynchronous movements of one claw or the other: both claws seem to start synchronously. Possibly, an increased slow-motion technique might reveal an ancestral alternating activation of one claw followed by that of the other one. In any case it becomes clear from the above facts that *Dotilla* has ascended a higher evolutionary ladder than *Macrophthalmus* as far as waving is concerned. In this context it is interesting to quote from a letter by Tweedie (1957) regarding the alternating or simultaneous use of the chelae in *D. myctiroides*: "I think I am right in my observation that *D. m.* uses its chelae both simultaneously and alternately". The situation in the realm of *Uca* must be considered separately, because the tendency of occupying a habitat by more than one often closely related or similar species is so prominent among these true fiddlers that strong evolutionary pressures may be expected to act on the mechanisms of species recognition and individual acquaintance: we have come across mud banks in the gulf of Guayaquil (Ecuador) where a 10 × 10 m square is inhabited by no less than 18 species of *Uca* in which interspecific recognition mechanisms are evident (Von Hagen 1968; Altevogt 1969, films 1967).

Waving in **Uca urvillei**

There is not much information in the literature about the behavioural ecology of this large steel-blue species (carapace width upto 36 mm) the most extensive report being that by Crane (1975). Hence, the following notes may also be taken as an addition to Crane's data (1975, pp. 58-61, table 19). Our findings are mainly based on fieldnotes and movies of 50 waves taken on the islands of Vypeen and Vallarpadam in the Bay of Cochin during March and in Goa (near Panaji) in April. Ovigerous females were numerous indicating that the mating season was in full swing. Nevertheless, waving by the males remained a slow affair indeed, and I know of no other true fiddler of such pronounced lethargy. Thus, the statement by Crane (1975) will remain valid: "Waving display among the simplest" (p. 59). As can be seen from fig. 3, the wave consists of a plain up-and-down of the claw in front of the body with a highest elevation just above the tip of the eyes. No body raise by leg stretching could be seen though in the frequent waving-cum-locomotion such a tip-toeing might seem to occur. That quite frequently waving is performed while marching may be taken as an indication for the still close neurophysiological correlation of walking legs and chelipeds (see Altevogt 1972) also suggesting that *U. urvillei* must be placed on a rather low phyletic scale. From fig. 3 the temporal components of the *urvillei*-wave at the highest arousal level can be seen lasting about 0.5 seconds in the upstroke and 0.17 seconds for the downstroke, making one complete wave last 0.67 seconds. This is slightly shorter than the 0.75 to 0.88 seconds mentioned by Crane (l.c.) and is probably attributable to the fact that in Crane's observations (in August/September) the peak of the mating season was not covered. As far as arousal stages are concerned (see Von Hagen, 1962), our courting males showed definite claw bleaching, with pollex and dactylus clear white and the manus sometimes included in this process. In most of the females also the two small claws became conspicuously white with advancing ebb tide. While Crane could not observe any copulations (apart from pseudocopulatory coverings of females by males),

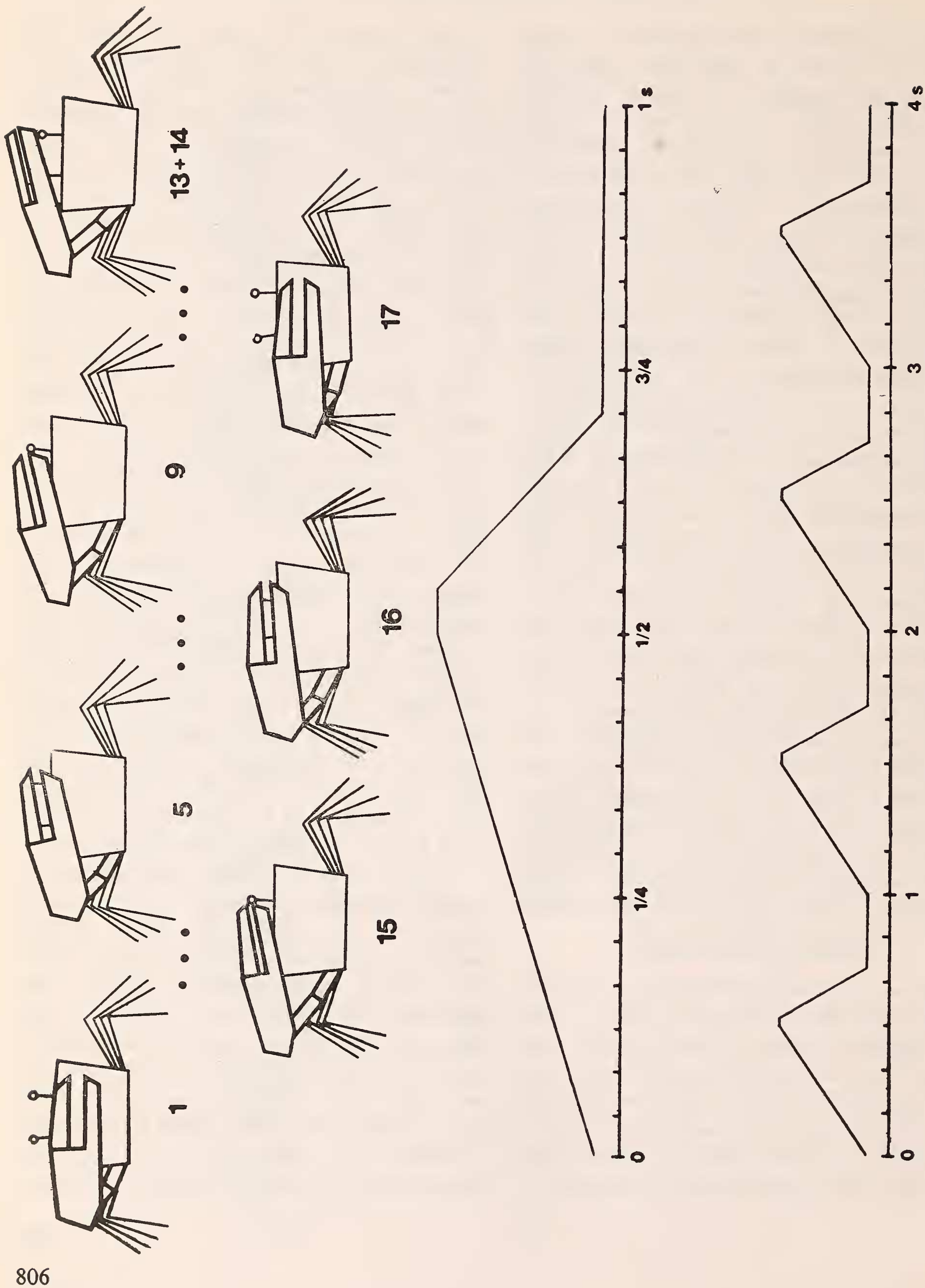

Fig. 3. Waving in *Uca urvillei*, frontal view. Numbers and dots in upper two lines represent frame number of movie (24 frames per second)—Time scale in lower two lines: 1/24 second.

during our study true copulations (above ground) were quite numerous lasting from 3 to 11 minutes. Some copulations were not preceded by any waving or precopulatory behaviour at all. Normally, though, about 7-11 waves in one series would be aimed at the receptive female, while in a non-courtship display such series consist only of 3 to 4 (as also mentioned by Crane).

It seems worthwhile to briefly compare the waving pattern of *U. urvillei* to that of *U. vocans* (formerly known as *U. marionis*, Holthuis, 1959), as both species are of about the same size and in some places the two species are sympatric (as in Goa and the Cochin region). As reported earlier (Altevogt, 1955, 1957, 1958, 1959), the wave in *U. vocans* follows the temporal and spatial patterns presented in fig. 4.

In both species the upstroke lasts longer than the downstroke, and it is the downstroke which carries the signal "potent male ready to copulate". Now, this informative element would be similar if not identical in both these species if it were not preceded by a different outward flexion angle of the great claw: in *urvillei* the claw is never flexed outward-laterally (see graphic presentation in fig. 3) while in *vocans* the claw's tip is raised high above the eye by a lateral-outward flexion. Moreover, in *vocans* the apex of a wave is emphasised by a body raise on tiptoe, which in *urvillei* was never seen. In *urvillei*, on the other hand, the apex, i.e., the highest position of the claw in the wave, seems to be more pronounced than in *vocans* which shows up in the graphic presentation of fig. 3 in that at this moment the claw is held for a short while (about 0.04 sec). Hence, in spite of all similarities in the timing of the two waves there are certain specific distinctions which undoubtedly serve the conspecific recognition in sympatric encounters.

This recognition of the conspecific sex partner is aided by the typical male waving dance around the female with the male's bleached back facing her. Such a crescendo is absent in *urvillei* so that also from this point of view *urvillei* must be placed between the proto-fiddlers and *Uca vocans* and the more highly evolved true fiddlers.

By the above remarks we hope to have related some examples of proto-fiddlers and lower true fiddlers by which evolution might have ascended to that high level of diversity

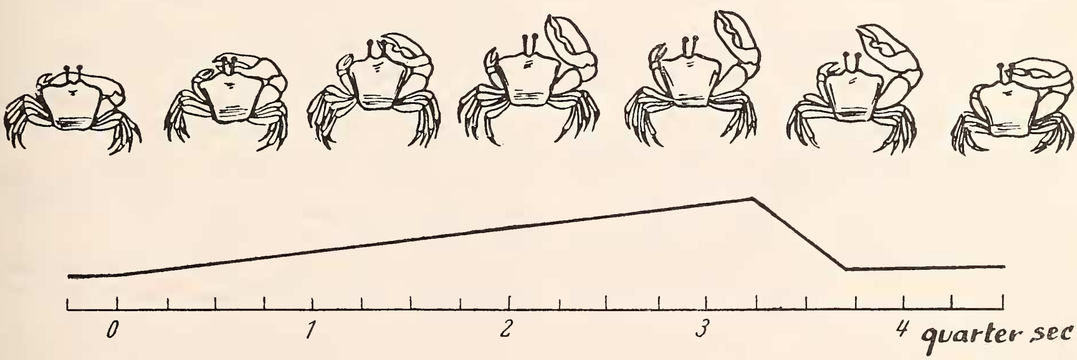

Fig. 4. Waving in *Uca vocans*, dorsal view. Time scale: 1/16 second (from Altevogt, 1955).

and complexity in the waving (and vibratory) signals which may be encountered in the field (For problems of "brachyurization" see also Stevcic 1971). A glimpse of this wealth may be gained from the films listed below which are on loan or for sale by the Institut fur den Wissenschaftlichen Film, Nonnenstieg 72, D-3400 Gottingen, Federal Republic of Germany.

Reference

ALOCOCK, A. (1892): On the habits of *Gelasimus annulipes*. Edw. *Ann. Mag. nat. Mist. 6*: 415-416.

——————— (1902): A Naturalist in Indian Seas. London, 328 pp.

ALTEVOGT, R. (1955): Some studies on two species of Indian fiddler crabs, *Uca marionis nitidus* (Dana) and *U. annulipes* (Latr.). *J. Bombay nat. Hist. Soc. 52*: 702-716.

——————— (1957a): Untersuchungen zur Biologie, Okologie und Physiologie indischer Winkerkrabben. *Z. Morph. Okol. Tiere 46*: 1-110.

——————— (1957b): Beitrage zur Biologie und Ethologie von *Dotilla blanfordi* Alcock und *Dotilla myctiroides* (Milne-Edwards) (Crustacea Decapoda). *Z. Morph. Okol. Tiere 46*: 369-388.

——————— (1959): The love and life of fiddler crabs. *J. Bombay nat. Hist. Soc. 56*: 1-7.

——————— (1969): Ein sexualethologischer Isolationsmechanismus bei sympatrischen *Uca*-Arten (Ocypodidae) des Ostpazifik. *forma et functio 1*: 238-249.

——————— (1972): Physiological inter-relations of display and locomotion in fiddler-crabs: An evolutionary aspect. *J. mar. biol. Ass. India 14*: 456-467.

CRANE, J. (1975): Fiddler crabs of the world. Ocypodidae: Genus *Uca*. Princeton Univ. Press, 736 pp.

FEEST, J. (1969): Morphophysiological studies on the ontogeny and sexual biology of *Uca annulipes* and *Uca triangularis* as compared to *Ilyoplax gangetica*. *forma et functio 1*: 159-225.

GUNTHER, H. J. (1963): Untersuchungen zur Verbreitung und Okologie von *Uca tangeri* an der SW-iberischen Kuste. *Z. Morph. Okol. Tiere 53*: 242-310.

HAGEN, H. O. VON (1962): Freilandstudien zur Sexual- und Fortpflanzungsokologie von *Uca tangeri* in Andalusien. *Z. Morph. Okol. Tiere 51*: 611-725.

——————— (1968): Studien an peruanischen Winkerkrabben (*Uca*). *Zool. Jb. Syst. 95*: 395-468.

HEDIGER, H. (1933): Notes sur la biologie d'un crabe de l'embouchure de l'Oued Bou Regreg, *Uca tangeri* (Eydoux). *Bull. Soc. Sci. nat. Maroc 13*: 254-259.

HEINRICH, B. (1971): Die Wirkung psychotroper Substanzen auf das Verhalten von *Uca tangeri*. *Zool. Beitr. (N.F.) 17*: 33-82.

HOLTHUIS, L. B. (1959): Notes on pre-Linnean carcinology (including the study of Xiphosura) of the Malay Archipelago. Chapter 5 in "Rumphius Memorial Volume", 63-125.

JANSEN, P. (1970): Physiologisch-okologische Untersuchungen zum "Posen" von *Uca tangeri*. *forma et functio 2*: 58-100.

KORTE, R. (1966): Untersuchungen zum Sehvermogen einiger Dekapoden, insbesondere von *Uca tangeri*. *Z. Morph. Okol. Tiere 58*: 1-37.

MCNAE, W., AND M. KALK (1958): A natural history of Inhaca Island, Mocambique, Johannesburg.

NOSLER, H. G. (1963): Ontogenese und Biologie von *Uca tangeri* (Eydoux). Thesis, Munster.

SCHONE, H., AND SCHONE, H. (1963): Balz und andere Verhaltensweisen der Mangrovekrabbe *Goniopsis cruentata* Latr. und das Winkverhalten der litoralen Brachyuren, *Z. Tierpsychol. 20*: 641-656.

STEVCIC, Z. (1971): The main features of brachyuran evolution. *Syst. Zool. 20*: 331-340.

TWEEDIE, M. W. F. (1954): Notes on grapsoid crabs from the Raffles Museum, Nos. 3, 4 and 5. *Bull. Raffles Mus. 25*: 118-127.

WRIGHT, H. O. (1968): Visual displays in brachyuran crabs: field and laboratory studies. *Am. Zool. 8*: 655-665.

Selected list of films on the behaviour and ecology of *Uca* species published by the Institut fur den Wissenschaftlichen Film, Nonnenstieg 72, D-3400 Gottingen, Federal Republic of Germany.

ALTEVOGT, R. (1957): Zur Biologie indischer Winkerkrabben. Film D 756.

ALTEVOGT, R., AND ALTEVOGT, R. (1967a): *Uca batuenta* (Ocypodidae). Balz. Film E 1292.

———— (1967b): *Uca insignis* (Ocypodidae). Balz. Film E 1288.

———— (1967c): *Uca stylifera* (Ocypodidae). Balz. Film E 1268.

HAGEN, H. O. VON (1971): *Uca maracoani* (Ocypodidae). Balz. Film E 1423.

———— (1972): *Uca cumulanta* (Ocypodidae). Balz. Film E 1420.